Variation in Communities of Seed-Dispersing Ants in Habitats with Different Disturbance in Knox County, Ohio[1]

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Abstract. Disturbance may disrupt mutualisms between plants and seed dispersers in a variety of ways including changes in the community of dispersers present. We tested the hypothesis that habitat alteration disrupts the seed-dispersal mutualism between ants and spring-flowering, perennial herbs. Fourteen study sites in Knox County, OH, represented a range of disturbance including mature woodland, woods recovering from partial logging up to 30 years prior to the study, recently logged woods, early successional field, and corn field. Baits were distributed among 480 positions in 48 randomly located transects. Ground-foraging ants were collected and vegetation characteristics of the transects were recorded. In 315 encounters of ants with baits, locations with tuna and seeds of the myrmecochore, *Sanguinaria canadensis*, were visited at equal rates. Visitation rates to the baits were higher in the more disturbed sites. There was little evidence for depressed ant diversity in disturbed habitats, though ant community composition varied. Seed dispersal distances were likely to be depressed only in agroecosystems, due to the smaller average size of ants, but even this difference is moderated by the tendency for myrmecochores in disturbed sites to have small seeds relative to plants in forest habitats. Where sites have extensive tree canopies the ant communities and dispersal rates are likely to be very resistant to change. Thus, habitat alteration may only affect the ant-plant seed dispersal mutualism in highly and continually disturbed habitats.

OHIO J SCI 103 (4):89–97, 2003

INTRODUCTION

Disturbance to ecosystems can change the nature of interactions between species as well as influence the composition of communities. Mutualism where seeds are dispersed by animals is one kind of interaction that might be particularly vulnerable to disturbance, whether that disturbance is caused by invasive species (Bond and Slingsby 1985; Zettler and others 2001; Christian 2001) or by habitat alteration that shifts the composition of species (Andersen and Morrison 1998).

Dispersal of seeds by ants (myrmecochory) involves many species of plants and ants in mesic habitats of North America (Beattie 1985; Hölldobler and Wilson 1990). Up to 30% of the ramets of spring-flowering, perennial herbs in these habitats are specialized for having their seeds carried by ground-foraging ants. Typical genera of plants with species using this dispersal syndrome include *Asarum, Claytonia, Dentaria, Dicentra, Erythronium, Jeffersonia, Sanguinaria, Trillium,* and *Viola.* Specialization for this mutualism involves plants producing small seeds that have a fat-rich aril (elaiosome). Although ants are not attracted from a distance to these seeds (Sheridan and others 1996), upon contact with the elaiosome, ants are stimulated to carry the elaiosome (and secondarily the attached seed) to their nests. There, the elaiosome is fed to larvae. Undamaged seeds can be deposited outside the nest or may become buried in the nest. Seed dispersal for these plants has both demographic (Hanzawa and others 1988; Kjellsson 1991) and genetic consequences (Kalisz and others 1999). Normally, ground-foraging ants collect insects from the leaf litter and ants are not obligately dependent on myrmecochory, but adding the food resource of elaiosomes can increase a nest's production of gynes (virgin queens) (Morales and Heithaus 1998). Producing more gynes is required for founding new colonies, so this is an important consequence.

Pudlo and others (1980) suggest that disturbance of a forest habitat decreases the diversity of ant fauna, including the numbers of seed-dispersing species, which eventually leads to a reduction in myrmecochorous plant species because of the loss of their seed-dispersing mutualists. In this study, we examined the hypothesis that disturbance disrupts the mutualistic system of myrmecochory. We sampled the ground-foraging ant community and the rate of discovery of baits in a series of habitats that represent a range of disturbance. We asked whether disturbance reduces the probability that ant-dispersed seeds are located and transported.

MATERIALS AND METHODS

Site Selection: Field work for this study was carried out from 23 May 1986 through 8 July 1986 in Knox County, OH. All sites were located within 8.0 km of Gambier, OH, USA. Potential sites were first located on recent aerial photographs obtained from the Ohio State Agricultural Extension Office. We used Sigma-Scan™ to digitize and measure areas of each site. Fifty potential sites were then visited, and fourteen sites were selected for study based on accessibility, availability of historical information, and representation across a range of disturbance. Three woodlots were sub-sampled to test for within-site variability, and samples within these different subsites were analyzed separately.

All sites were located on ground moraine deposited by the Wisconsin or Illinoisan glaciers, on upland habitats.

[1]Manuscript received 20 November 2001 and in revised form 1 July 2002 (#01-31).

Historically, these sites would have been occupied by mixed, deciduous forest (especially *Quercus*, *Acer*, *Fagus*, and *Carya*). All sites had been modified by some degree of timbering, but they varied in the time since the last harvest, the amount of canopy removed, and the use of the land after removal of trees.

Sites were characterized for "degree of disturbance" using parameters that literature suggests are important for ant communities (canopy closure, litter coverage, and understory coverage). The categories were "Least Disturbed," "Moderately Disturbed," and "Open or Mostly Open Canopy." Site descriptions follow and site characteristics are compared in Table 1.

Low Disturbance

All sites had closed canopy on the 1940 aerial photographs. The understory was comprised of perennial herbs and scattered saplings, with a well-developed layer of leaf litter. Myrmecochores comprised about one-quarter of the species of understory perennial herbs.

"Burns" – This woodlot had remained undisturbed for 30 yr (neither grazing nor selective cutting). Prior to that time, the site had been grazed and selectively cut for oak. The canopy over transects was closed and dominated by *Acer saccharum* and *Quercus alba*, with large *Fagus grandifolia* near but not over the transects.

"Sapp" – The canopy was closed and dominated by *Acer saccharum*, *Carya ovata*, and *Fraxinus americana*; the understory included six species of myrmecochorous plants, and the density of myrmecochores was high.

"Crouch" – The canopy was closed at the time of sampling. *Acer saccharum* and *Quercus rubra* dominated trees.

Moderate Disturbance

These sites had varying history, but generally there was evidence of more extensive or more recent timber removal than for the Least Disturbed sites. The proportion of myrmecochores in the understory varied, but low frequencies were interpreted as another indication of historical disturbance (see Matlack 1994; Jessen 2000).

"Baube" – This site may have been cleared for row crops prior to 1940, but the canopy was continuous at the time of sampling. Trees tended to be even-aged and dominated by *Fraxinus americana* and *Ulmus rubra*

"Heithaus" – This closed-canopy site had been selectively cut at a high intensity prior to 1940, and then selectively cut at a low intensity about fifteen years prior to sampling. Trees were co-dominated by *Fraxinus americana*, *Ulmus rubra*, and *Acer saccharum*.

"Backbone" – Located on the Brown Family Environmental Center at Kenyon College, this woodlot in 1940 consisted of clumps of trees with many open areas. Many of the largest trees (dominated by *Quercus alba* and *Carya glabra*) were planted in a forest management program in 1912, and the canopy was continuous at the time of sampling.

"Biology" – A narrow section of closed-canopy woods between the main campus of Kenyon College and State Route 229. The site is more exposed than most other sites to trampling. The trees were dominated by

TABLE 1

Characteristics of study sites in Knox County, OH. "Ground Cover" was calculated using a line intercept method along 20 m segments of each transect. "Largest Tree Diameters" is the mean diameter of the three largest trees intersecting each transect. "Percent Myrmecochore" reflects the proportion of species of understory herbs along transects that have their seeds dispersed by ants. See text for definitions of disturbance categories.

Site	Area (ha)	W. Long/N. Lat	Number of Transects	% Ground Cover	Largest Tree Diameters (cm)	Number of Myrmecochores	Percent Myrmecochores	Disturbance Category
Burns	247	82.377/40.358	6	50	85	6	27	low
Sapp	101	82.320/40.404	6	45	59	6	28	low
Crouch	74	82.401/40.337	2	20	61	4	24	low
Baube	247	82.376/40.356	3	65	43	2	13	moderate
Heithaus	153	82.419/40.400	2	27	48	3	25	moderate
Backbone	148	82.418/40.383	4	42	92	1	13	moderate
Biology	90	82.400/40.372	2	59	65	1	13	moderate
Magers	74	82.405/40.334	2	44	54	2	16	moderate
Lepley	35	82.373/40.391	6	55	54	1	8	moderate
McPhail	30	82.356/40.362	5	45	63	2	30	moderate
Prescott	252	82.429/40.402	3	66	63	3	20	high
Blanchard	153	82.413/40.395	2	95	44	1	5	high
Corn	99	82.359/40.363	2	0	0	0	0	open
Field	15	82.419/40.400	3	100	0	0	0	open

Quercus alba.

"Mager" – Major overstory trees were *Acer saccharum, Ulmus rubra,* and *Quercus velutina.* The understory included two species of myrmecochorous plants. The canopy was continuous in 1940, but some cutting of timber had occurred.

"Lepley" – The canopy was closed and dominated by *Acer saccharum, Carya ovata,* and *Fraxinus americana.*

"McPhail" – Although the canopy was mostly closed, tree stumps indicated moderately intensive, selective cutting in the last decade. Understory vegetation was denser than in most other, forested sites. The most common trees over transects were *Acer saccharum, Ulmus rubra,* and *Prunus serotina.*

High Disturbance

These sites had major portions of the canopy removed within the last two years. Remnants of the understory were present, but logging activity disrupted the soil surface. Sampling attempted to avoid downed wood and tracks in the soil left by heavy equipment.

"Prescott" – This site is adjacent to a state nature preserve, Knox Woods. Numerous large trees were removed in the spring just prior to sampling (approximately a 40% cut). *Prunus serotina* and *Acer rubra* dominated the remaining overstory.

"Blanchard" – Most trees were removed from this site one year prior to sampling. Much of the understory was dominated by ruderal species, including *Rosa multiflora.*

Open Canopy

These sites had no trees, and the ground-level vegetation was quite different from that of forested areas.

"Corn" – A cornfield adjacent to the McPhail wooded site, approximately 25 m from the forest edge. Conventional tillage was used in this site.

"Field" – An old field approximately 200 m from the transects in "Heithaus" and adjacent to that woodlot. The field had been mowed in April and twice a year for the six years prior to sampling. Grasses, *Solidago* spp., and *Aster* spp. dominated the site.

Transect Location: Transects of 40 meters were established in all sites for both ant and vegetation sampling (see Table 1 for the distribution of transects among sites). To establish transects, we stopped at a haphazard point within the study area. To establish the start of a transect, we then selected a random distance and compass direction (1-360 degrees from north) from a table of random numbers to establish the transects starting point. Then, the direction of the transect from the starting point was, again, selected from a table of random numbers. The number of transects per site is indicated in Table 1.

Habitat Characterization: All herbaceous species within 1.0 m of a transect were identified and species' presence noted. The percentage of each transect covered by herbaceous flora ("percent cover") was determined by counting the number of times a leaf of an herb was above or below a decimeter division of alternating meters along the 40-m transect. All trees that had a branch or leaf overhanging the transect were identified, their location on the transect noted, and their diameters "at breast height" measured. The density and dominance of each species of tree in a transect were calculated and importance values were obtained for each species.

Ant Sampling: Most sampling was done between 10:00 and 14:00 hr. Air and soil surface temperatures were recorded, and we generally attempted to sample ants when the air temperature was at least 20° C.

Baits were either tuna (canned in oil) or seeds of the myrmecochore, *Sanguinaria canadensis.* Seeds of *S. canadensis* were collected from 1-7 June and stored in vials with BHT crystals at 5° C until the day of sampling, a treatment that preserves attractiveness to ants (Heithaus 1986). Baits were placed at ten, randomly selected points (using a random numbers table) along each 40-m transect. At all sites, similar amounts of tuna were placed on leaf litter or other visible location (for example, bare ground) at each point. Seeds of *S. canadensis* were used in additional transects at nine sites (ten seeds per point). Baits were monitored at least at 15 min intervals for at least 2 hr. A total of 480 bait stations were used.

When ants were first found at a bait, the time of discovery of that bait was noted. Ants were observed to note their response to the bait (whether it was being investigated or carried) and whether recruitment was occurring. Occasionally, individual ants were followed back to their nests and the distance to the nest was noted. Ants were collected from baits using an aspirator and then killed in cyanide-containing jars.

To supplement collections at baits, we collected ants near, but further than 2.0 m from transects. Visual inspection of ground, vegetation, and litter was done in the time intervals between monitoring transects, for up to 90 min of searching per transect. Ants encountered in these searches were collected with an aspirator and kept separate from collections at baits. This was done to test whether we were missing common species of ants by sampling with tuna and seed baits; visual searching was not intended to be quantitative.

In the laboratory, each ant was mounted on a triangular paper point on an insect pin and the specimen was labeled for date, site, location, bait, and transect point. Ants were identified to genus using Creighton (1950). D. R. Smith kindly identified ants to species; reference specimens are deposited in his collection at the Smithsonian Institution and at the Brown Family Environmental Center at Kenyon College. An ocular micrometer was used to measure alitrunk lengths for up to ten individuals of each species. The length of the alitrunk was used as an index of body size because this is reported in other studies and it appears to be functionally related to an ant's ability to carry loads of different sizes.

Statistical Analysis: Statistical analysis was done with JMP IN® 4.0.3 (Academic Version). The proportions of baits located by ants were arcsine transformed before statistical analysis, because raw proportions were not distributed normally. Confidence limits reported are back-

transformed values. The models for analysis of variance treated sites as nested within disturbance category, and disturbance category as a random effect. Log-Likelihood (G) tests were used for analysis of frequencies (Zar 1999). Species diversity of ants was characterized with the program, EstimateS (Colwell 1997).

RESULTS

From the perspective of an ant-dispersed seed, three questions are important in addressing the quality of seed dispersal services. These are: Will a seed be discovered? Will the seed be moved away from the parent plant? To what microsite will the seed be moved? Here, we present our data in terms of these questions.

The type of bait did not influence the probability that ants would be found at a transect point. This question was addressed by examining the frequency of baits visited by ants, where bait type was nested within site and site effects were included in the model, and also by comparing the frequencies of ant species visiting baits in sites where both types of bait were offered. Tuna and seed baits were similar in the probability of being located by ants ($F = 0.65$, $df = 9$, $P = 0.74$), and in the composition of the ant community visiting the baits ($G = 0.02$, $P > 0.995$). Consequently, bait types were ignored as a variable when examining questions about the effects of disturbance and temperature on ant visitation patterns.

Both the category of disturbance and differences among sites within these categories influenced the visitation of baits by ants (Fig. 1, Table 2). In the sites with little or no shading from trees, nearly all the baits were visited. In sites with a tree canopy, whether the disturbance was "least" or "moderate," about half the baits were visited in the sampling period. Disturbance category explained 45.5% of the variation in visitation frequency ($F = 7.31$, $df = 3$, $P = 0.0007$). Given the difficulty in categorizing "disturbance," variation among sites within these categories is expected ($F = 4.62$, $df = 11$, $P = 0.0002$). For example, among "moderately disturbed" sites, the visitation rate varied from 13% to 83%, although transects within sites tended to be much more consistent. Much less variation in visitation was observed in the sites with more open canopies, as ants located most baits in those sites.

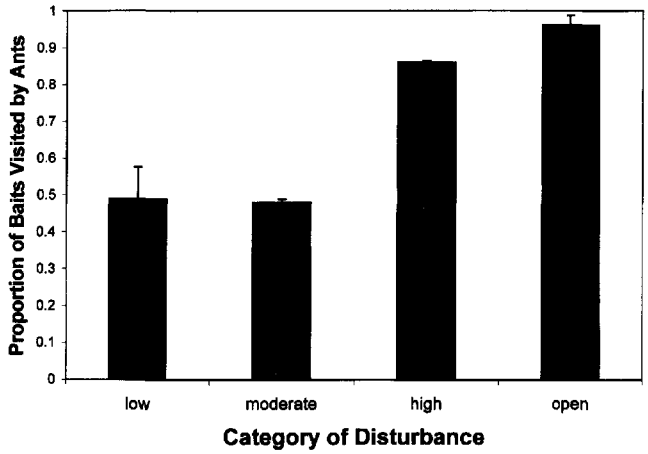

FIGURE 1. Probability of a bait being visited by ants in sites with different histories of disturbance. Error bars represent one standard error, back transformed from the arc-sine transformation used in statistical analysis. The probability of visitation was influenced by disturbance history ($F = 7.31$, $df = 3$, $P = .0007$) and by sites nested within category of disturbance ($F = 4.62$, $df = 11$, $P = .0002$). Disturbance accounts for 45.5% of variation in visitation frequency. "Open" and "High" disturbance sites were similar but different than "Moderate" and "Low" disturbance sites (Tukey HSD, $p < 0.05$).

TABLE 2

The rate of visitation to baits among different sites. Visitation varied among sites within category of disturbance ($F = 4.62$, $df = 11$, $P = 0.0002$).

Site	Disturbance	Prop Visited	S.E.
Burns	least	0.35	0.016
Sapp	least	0.45	0.014
Crouch	least	1.00	0.0
Baube	moderate	0.13	0.024
Heithaus	moderate	0.65	0.003
Backbone	moderate	0.42	0.016
Biology	moderate	0.55	0.003
Magers	moderate	0.40	0.044
Lepley	moderate	0.83	0.034
McPhail	moderate	0.26	0.023
Prescott	high	0.90	0.019
Blanchard	high	0.80	0.113
Corn	open	0.90	0.0
Field	open	1.00	0.0

Higher soil surface temperatures in treeless sites may account for some of the differences in bait discovery among sites. Transects in "open" sites averaged 26.5° C, while soil surface temperatures in sites for all other categories of disturbance ranged from 18.7 to 20.3° C (in proportion to the openness of the canopy). Only the "open" sites were statistically distinct from any other sites ($F = 12.39$, $df = 3$, $P < 0.0001$), so soil surface temperature alone cannot explain the higher rate of visitation to baits in the highly disturbed sites compared to other forested sites.

We asked whether removal rates of *Sanguinaria canadensis* seeds varied with disturbance and site. The question is important because plants tend to deposit many seeds in a locality, and dispersal success is influenced by whether ants remove all, or just a fraction, of the available seeds in that locality. For this analysis, we used only transects with seeds, and we evaluated the number of seeds removed if the transect site was visited by ants (Fig. 2). Seven sites had seed baits visited (2 - 12 baits among sites). Of the ten available seeds per baiting station, ants removed an average of from 4.1 (Burns) to 9.8 seeds (Field). Due to the high number of seeds removed from the open, field site, removal rates were significantly influenced by disturbance category ($F =$

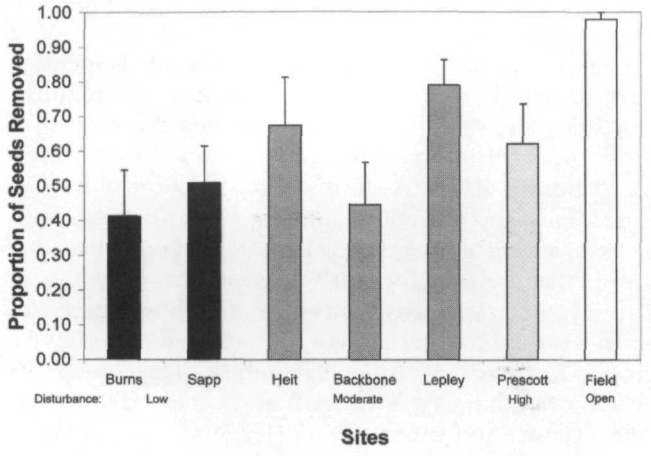

FIGURE 2. Proportions of *Sanguinaria canadensis* seeds removed if seed-baits were discovered. Error bars represent a single standard error. Disturbance category (sites nested within disturbance) influenced seed removal ($F = 4.30$, $P = 0.008$).

4.30, df = 3, $P = 0.008$), and this factor accounted for 25% of the variability in seed removal rates. The general trend was for increasing removal rates in more disturbed habitats as just described, and for relatively low variability in seed removal among sites within disturbance category as indicated by the marginally insignificant effect of sites nested within disturbance categories ($F = 2.48$, df = 3, $P = 0.07$).

Another approach to predicting whether seeds will be removed is to evaluate the composition and characteristics of the ant community that would be attracted to seeds.

Twenty-two species of ants were collected in 315 encounters (Table 3). One indication of sampling effectiveness over the entire study is the fact that no additional species of ground-foraging ants were collected in sampling away from baits. Of 95 collections away from baits, only *Protomognathus* (=*Harpagoxenus*) *americanus* was newly encountered; this slave-making species would not be expected to visit baits. Within the forest sites, we encountered seventeen species of ants, and the accumulation curve for the Shannon Index (Fig. 3) indicated sufficient sampling for this parameter over all the sites (Colwell 1997). Within sites, however, due to the low activity of ants, we encountered relatively few individuals and we predict that much more extensive sampling would yield more species (Colwell and Coddington 1994). This would not alter the primary trends identified in this study.

Although all the sampled species of ants are likely to respond to seeds (given that they were attracted to these baits), they also are likely to vary in their behavior with respect to seeds. Ants can vary in whether elaiosomes are detached *in situ* or whole seeds are transported, and in the distances and destinations of seeds if seeds are transported. These issues will be examined more critically in the discussion, but the size of an ant is one factor influencing its ability to transport a seed. Ant size also is correlated with the foraging distances from nests, a factor influencing transport distance (Hölldobler and Wilson 1990; Weseloh 1994; Gómez and Espadaler 1998a). Among the ants we collected, there was nearly a six-fold increase in alitrunk length from the smallest species (*Solenopsis molesta*) to the largest (*Camponotus pennsylvanicus*). With the exception of ants in the cornfield, all sites showed a large range in sizes of ant species. Although the most disturbed, open sites tended to have smaller species of ants (Table 3), successional field transects also were patrolled by *Formica* spp., which are

TABLE 3

The frequency of baits visited by ants in fourteen sites (see Table 1) in Knox County, OH, and alitrunk lengths (in mm) for observed species. Species are ordered by alitrunk length. The 315 visits were to 480 bait stations over 48 transects (some baits were visited by more than one species of ant). Of 95 collections of ants away from baits, only one additional species was encountered (Protomognathus (=Harpagoxenus) americanus *in a moderately disturbed site). Average sizes of ants were calculated considering frequency (weighted mean alitrunk length) and simply by observed species (unweighted mean alitrunk length).*

Species attracted to baits	Disturbance Category Low	Mod	High	Open	Length of Alitrunk (mm)
Camponotus pennsylvanicus	3	9	4	0	3.25
Camponotus ferrugineus	4	6	1	0	3.10
Formica subsericea	0	0	1	7	2.25
Camponotus nearcticus	0	1	0	0	2.20
Formica pallidefulva nitidiventris	0	0	0	3	2.00
Aphaenogaster tennesseensis	1	0	0	0	1.63
Aphaenogaster rudis	61	67	28	9	1.53
Camponotus subbarbatus	0	1	0	0	1.56
Myrmica lobicornis fracticornis	0	0	0	1	1.28
Lasius umbratus	0	2	0	0	1.16
Myrmica americana	0	1	0	14	1.15
Myrmica punctiventris	1	19	10	0	1.03
Prenolepis imparis	0	0	0	1	0.96
Tapinoma sessile	0	1	0	11	0.93
Lasius alienus	1	16	4	18	0.85
Lasius neoniger	0	0	0	1	0.80
Stenamma brevicorne	0	1	0	1	0.77
Stenamma impar	0	1	0	0	0.77
Stenamma schmittii	0	1	0	0	0.70
Leptothorax longispinosus	0	1	0	0	0.70
Leptothorax curvispinosus	1	2	0	0	0.65
Solenopsis molesta	0	0	0	1	0.44
Weighted mean alitrunk lengths	1.66	1.52	1.56	1.21	
Unweighted mean alitrunk lngths	1.72	1.39	2.00	1.18	
Number of baits visited	72	129	48	67	
Number of species	7	15	6	10	
Number unique species	1	6	0	4	

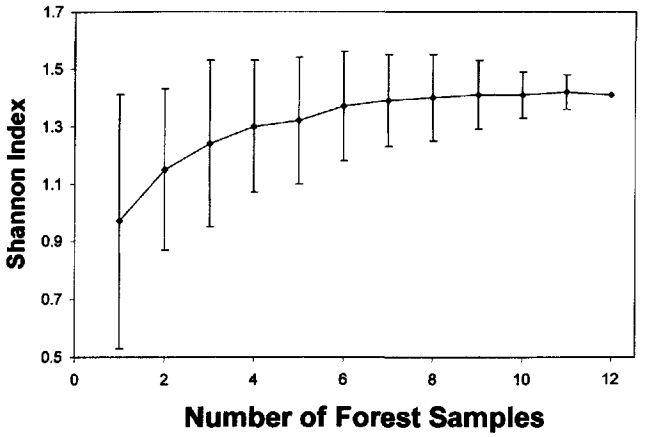

FIGURE 3. Accumulation curve for the Shannon Index, generated by EstimateS (Colwell 1997) through random resampling of data on ants collected at tuna and seed baits in Knox County, OH. Error bars represent one standard deviation.

capable of handling the largest myrmecochorous seeds in our area.

Are seed-carrying ants likely to transport seeds between habitat types? Destinations are a function of both foraging distance and nest location (including habitat specialization), as well as ability of a worker to return the seed to her nest. For species visiting at least 15 baits, analyses of frequencies (G tests) were used to test the null hypothesis of equal distribution among baits in different disturbance categories (P values are Bonferroni corrected for multiple comparisons). Some of the largest species in our study were either restricted to forest areas (*Camponotus* spp. [$G = 8.12$, $df = 3$, $P < .05$], *Myrmica punctiventris* [$G = 29.7$, $df = 3$, $P < 0.05$]) or were concentrated in sites with grasses and forbs (*Formica* spp. [insufficient sample for a statistical comparison]). Among the larger ants, *Aphaenogaster rudis* was found in nearly all types of habitats, but it was under-represented in open sites and over-represented in the least disturbed sites relative to the number of baits used ($G = 26.0$, $df = 3$, $P < 0.05$). Many of the smaller species were highly concentrated in the more disturbed sites (for example, *Myrmica americana* [$G = 61.2$, $df = 3$, $P < 0.01$], *Tapinoma sessile* [$G = 46.6$, $df = 3$, $P < 0.01$]). *Lasius alienus* was over-represented in the most disturbed sites, relative to sampling effort [$G = 47.9$, $df = 3$, $P < 0.01$], but was found in both forested and open sites.

DISCUSSION

Sampling Issues. Numerous studies indicate that a thorough sampling of ant communities includes litter sampling (Winkler extractions) or pitfall trapping, so it is important to emphasize here that our goal in using baits was to evaluate the foraging activity of ants likely to interact with myrmecochorous seeds. When research has included multiple techniques, few additional species are seen at baits after compiling species lists from pitfall traps and litter extractions (Delabie and others 2000; Wang and others 2001). Also, Bestelmeyer and others (2000) recommend baits as a reasonable measure of ant foraging efficiency. We emphasize that our discussion about "ant community" refers to that set of ants that might interact with elaiosome-bearing seeds.

The set of ants that interact with these seeds includes most, if not all, of the guild of "ground-foraging ants." Our study shows virtual identity between the species of ants collecting tuna and those attracted to myrmecochorous seeds. A study of the reaction of ants to elaiosomes and chemical analysis of elaiosomes suggests a strong convergence between elaiosomes and insects that are prey for ants (Hughes and others 1994). The seventeen species of ants collected in wooded sites in this study compare favorably to other studies of ground-foraging ants in similar habitats (Herbers 1985; Lynch and others 1988; Kaspari and others 2000; Ward 2000; Soares and others 2001; Herbers, pers. comm.). Although some might expect that more ants should have been found in the wooded compared to the open sites, relatively low abundance of ants in forest areas is consistent with the findings of Ferguson (2001).

Monitoring baits for 2 hr appears to allow sufficient time to sample the most common species of ants based on species-accumulation curves and is consistent with that used in other studies using baits. Some caution, however, should be used in interpreting the frequencies of bait discovery with 2 hr monitoring time because the discovery rates are not exactly equivalent to the probability that a bait (or depot of myrmecochorous seeds) would be found eventually. Variation in eventual discovery can arise because ant density can be locally patchy (Weseloh 1994; Weseloh 1995; Kaspari 2001), or because alternative foods are locally common (Smith and others 1989). We use frequencies of discovery for comparative purposes in this paper. We also believe that a 2 hr period is biologically significant because even relatively short delays of several hours in discovery can negatively impact seeds. This is because seeds are then more vulnerable to seed predators such as day-foraging chipmunks or night-foraging deer mice (Heithaus 1981).

Disturbance and the Response of Ground-foraging Ants: Our results suggest that the community of potential seed-carrying ants responds to disturbance over a large spectrum (for example, comparing corn fields, early succession, and wooded sites), but that within wooded sites only small responses are seen as long as the habitat retains substantial shading from a tree overstory. The composition of ant communities changed qualitatively from wooded to open habitats, but only quantitatively within wooded habitats. Potential mechanisms by which disturbance might alter ant communities are through changes in temperature, plant productivity, and the availability of specialized nesting sites (Kaspari 2000; Kaspari 2001). In some ecosystems, habitat specialization appears to be more important than competition in influencing the composition of ant communities at a local scale (Soares and others 2001).

Recently, considerable attention has been given to the responses of ant communities to disturbance both to understand patterns of biodiversity and to assess the potential for using ants as bioindicators (Agosti and others 2000; Kaspari and Majer 2000). A comprehensive

review is inappropriate here, but published studies show considerable variation in how ants respond to disturbance. Whether the composition of ant communities responds to disturbance depends, in part, on the ecosystem examined and the extent of disturbance (Roth and others 1994; Andersen 1995; King and others 1998; Peck and others 1998; Whitford and others 1999; Read and Andersen 2000; and Vasconcelos and others 2000). In mesic, forested ecosystems, disturbance can alter ant community composition although ant diversity may not vary substantially (Jennings and others 1986; Kidd and Longair 1997). This is consistent with our results. A thorough community sampling in Knox County woodlots (including all guilds, and not just ground-foragers) might reveal more response of ants to disturbance, but our study supports the view that ground-foraging ants that are potential seed-dispersers are not particularly sensitive to disturbance within wooded habitats. The guild of ground-foragers does change with major alterations in the forest canopy, however, one would not need to sample ants to detect the loss of forest canopy.

The Potential Effect of Varying Ant Communities on Seed Dispersal: Given that the guild of ground-foraging ants occurs in abundance across a wide variety of disturbance regimes, how might shifts in community composition influence the seed-dispersal mutualism? In fynbos shrublands of South Africa, the compositions of plant communities have changed as a result of changes in seed dispersal due to invasion and dominance of a small-bodied ant species (Christian 2001). In the mesic habitats of central Ohio, whether differences in ant communities have a similar effect depends on the degree to which different species of ground-foraging ants are interchangeable from the perspective of seed movement. Although species within this guild are likely to be attracted to seeds, there is interspecific variation in whether seeds are carried, how far seeds are carried, and how seeds are treated and deposited after removal from their original site of deposition (for example, Culver and Beattie 1978; Gorb and Gorb 1999b). Worker size, tendency to recruit, and colony structure are important variables. Small species of ants tend to remove parts of elaiosomes from large-seeded plants, rather than attempt to carry whole seeds (Espadaler and Gómez 1997; Andersen and Morrison 1998), and worker size strongly influences dispersal distance (Beattie and others 1979; Pudlo and others 1980; Weseloh 1994; Gómez and Espadaler 1998b). In part, the relative size of ants and seeds is important because foraging distances tend to be smaller for small-bodied ants (Hölldobler and Wilson 1990; Weseloh 1994; Gómez and Espadaler 1998a), but also because small ants more frequently drop seeds before they return to their nest (Gorb and Gorb 1999a). For different species of ants, average seed dispersal distances can vary from a centimeter to several meters; worldwide, the average seed dispersal distance based on carrying by ants is under 1.0 m (Gómez and Espadaler 1998a). For colonizing new sites, the "tail" of the dispersal curve may be more important than the average distance a seed might be carried. Extreme distances that ants carry seeds vary from centimeters to approximately 20 m. In temperate, broadleaf forests, dispersal distances average less than a meter, though large-bodied *Camponotus* spp. sometimes carry seeds 20 m (personal obs.). Finally, ants may differ in how seeds are treated after elaiosomes are removed in the nest by larvae (Beattie and Culver 1982; Heithaus 1986; Gorb and others 2000). To summarize, different species of ground-foraging ants show orders of magnitude differences in proportions of seeds removed and distances seeds are carried, and they vary in other parameters of interacting with seeds (though the impacts of those differences on plant evolution and demography is yet to be determined [Beattie 1991]).

How might differences in communities of ground-foraging ants in Knox County affect the dispersal of myrmecochorous seeds? In spite of their different ant communities and disturbance histories, a row-cropped agroecosystem, an early successional field, and diverse wooded areas differ little in whether myrmecochorous seeds are likely to be encountered and dispersed by ants. Although apparently in conflict with the conclusions of Pudlo and others (1980), our results are not strictly comparable. Their three study sites were at different altitudes or in different states (West Virginia and Illinois), and the most disturbed site included flooding events; while our study was within a single county and disturbance did not include flooding (which is more likely than forest clearing to have major, negative effects on ants). Their study examined dispersal of *Sanguinaria canadensis* seeds, which are at the large end of the range in size for myrmecochores; this would be expected to be among the most sensitive plants to variation in ant communities. In our study, we measured whether ants would encounter depots of any species of myrmecochore. For example, in our agroecosystem, where ant species tend to be smaller, local myrmecochorous plants (for example, *Viola* spp.) also tend to have small seeds, so that dispersal is likely to be successful for these more ruderal species. In fact, the foraging activity of ants tends to be high in the more exposed habitats (also see Bestelmeyer 1997), so dispersal frequency (if not distance) may be higher in more disturbed habitats. Myrmecochory, as a general dispersal strategy, should be successful within a wide range of habitats in Knox County. A similar result has been found in a range of sites and habitats in Australia (Andersen and Morrison 1998). The prediction for particular plant species, however, depends on the size of their seeds and the need for distance dispersal.

Ants appear to be poor promoters of colonization for plants. In addition to transporting seeds short distances, ants are relatively specialized in their choices of microhabitats or habitats (Hölldobler and Wilson 1990; Soares and Schoereder 2001). Studies of plant colonization in disturbed areas show that ant-dispersed plants are slow to move into restored or recovering sites compared to species with other seed dispersal mechanisms (Matlack 1994; McLachlan and Bazely 2001).

The seed-ant mutualism, as a general adaptation, is apparently quite resilient. Plants that have adapted to conditions of disturbance (particularly those with small

seeds) are likely to have their seeds dispersed. For forest species with relatively large seeds, however, new disturbance may negatively affect dispersal through the disproportionate loss of large-bodied ants from the local community. The long-distance colonization of new sites through other types of habitats appears to be much less likely. For plants adapted to old-growth forests, dispersal by ants probably could carry seeds into sites disturbed by selective logging. Here, the limit to colonization of moderately disturbed sites appears to be based on distance, not the habitat specialization of ground-foraging ants.

ACKNOWLEDGMENTS. Thanks to Greg Mosolf and Patricia Heithaus for assisting with vegetation sampling and other fieldwork. Thanks also to Michael Heithaus, Joan Herbers, and an anonymous reviewer for suggestions that improved this manuscript. Kenyon College supported research for this project through its Summer Science Scholarship program for undergraduate research.

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